



REVIEW

Drivers and facilitators of hunting behaviour in domestic cats and options for management

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ABSTRACT

1. Domestic cats *Felis catus* are distinct from other domesticated animals because their phenotype and genotype are relatively unchanged. While they live with people as pets or pest controllers, they retain capacity for survival independent of human support and readily persist as feral animals. Most cats retain some propensity to express hunting behaviours, even if hunting is not required for nutrition. In some settings, depredation by cats is a threat to biodiversity conservation, leading to attempts to mitigate their impacts.
2. We characterise drivers and facilitators of the hunting behaviour of domestic cats: evolutionary origins, diet, life history, personality and environment. Hunting is driven particularly by evolutionary constraints and associated physiological and nutritional requirements. Proximate causes of variation in hunting behaviours relate to prey availability, husbandry and degree of domestication, while early life history and personality play further roles.
3. We review cat management approaches in terms of effectiveness, feasibility and welfare. Amongst lethal, large-scale methods of population control, poisoning is most frequently used in cat eradications from islands. Because poisoning is challenged on welfare grounds, euthanasia is used at smaller scales and in inhabited, mainland settings. Non-lethal approaches, primarily surgical sterilisation, are favoured by cat advocates but entail challenging logistics and scale. In attempts to inhibit predation of wild species by pet cats, owners restrict outdoor access and use collar-mounted devices, including bells, sonic devices, collar covers and bibs. Other individual-level interventions, such as dietary and behavioural enrichment, some of which may improve cat welfare, have potential, but effects on hunting remain untested.
4. Understanding and managing the hunting behaviour of cats are complex challenges. We highlight drivers and facilitators of this behaviour, representing starting points for formulating solutions that might be acceptable to cat owners and wider groups of people who value cat welfare, while also being effective for wildlife conservation.

Parole chiave

ecologia degli animali da compagnia, gatto domestico, *Felis catus*, gatto feroce, gestione, predazione, conservazione della fauna selvatica

RIASSUNTO IN ITALIANO

1. I gatti domestici *Felis catus* si distinguono dagli altri animali domestici poiché i loro fenotipo e genotipo sono rimasti relativamente invariati. Nonostante vivano con le persone come animali domestici o vengano impiegati per il controllo dei roditori infestanti, i gatti domestici hanno mantenuto la capacità

di sopravvivere indipendentemente dal supporto umano, e possono facilmente persistere come animali ferali (rinselvaticiti). La maggior parte dei gatti ha mantenuto una certa propensione alla caccia, nonostante questa non sia necessaria a sopperire a esigenze nutrizionali. In determinati ecosistemi la massiccia predazione da parte dei gatti rappresenta una minaccia per la conservazione della biodiversità, determinando quindi la necessità di adottare soluzioni per mitigare i possibili effetti negativi.

2. In questo studio vengono caratterizzati i fattori chiave che inducono i gatti domestici a cacciare, nonché quelli che ne facilitano l'espressione: le origini evolutive, il regime alimentare, le esperienze fatte nel corso della vita, la personalità e l'ambiente. Il comportamento di caccia è primariamente determinato da vincoli evolutivi e da fabbisogni fisiologici e nutrizionali ad esso associati. Le cause prossime coinvolte nelle variazioni di tale comportamento sono legate alla disponibilità di prede, dal metodo di allevamento del gatto e dal suo grado di addomesticamento; le esperienze fatte nei primi mesi di vita e la personalità del gatto ricoprono anch'essi un ruolo importante.
3. Abbiamo revisionato i diversi approcci impiegati nella gestione dei gatti in termini di efficacia, fattibilità e benessere. Tra i metodi letali impiegati su larga scala nel controllo di popolazione, l'avvelenamento è risultato essere quello più frequentemente utilizzato per l'eradicazione dei gatti dalle isole. Poiché l'avvelenamento è contestato per motivi legati al benessere, su scala più piccola e in posti abitati sulla terraferma viene preferita l'eutanasia. Gli approcci non letali, in particolare la sterilizzazione chirurgica, sono favoriti dai sostenitori dei diritti dei gatti, ma implicano complicazioni sul piano logistico e risultano comunque essere di portata più limitata. Nel tentativo di inibire la predazione dei gatti domestici sulle specie selvatiche, i proprietari ne limitano l'accesso all'esterno e utilizzano dispositivi che si attaccano ai collari, come campanelle, dispositivi sonori, copri collari colorati e bavagli ingombranti. Altri interventi a livello individuale come, ad esempio, l'arricchimento alimentare e quello comportamentale hanno un potenziale (alcuni potrebbero incrementare il benessere del gatto stesso), ma gli effetti sul comportamento di caccia non sono stati ancora testati.
4. La comprensione e la gestione del comportamento di caccia dei gatti rappresentano delle sfide complesse. Il presente lavoro evidenzia i fattori che guidano e quelli che facilitano tale comportamento, che rappresentano i punti di partenza per formulare soluzioni che potrebbero essere accettate dai proprietari dei gatti e da tutte le persone che ne valorizzano il benessere, e che al contempo siano efficaci nel salvaguardare gli animali selvatici.

INTRODUCTION

Relationships between domestic cats *Felis catus* and people have evolved over millennia (Serpell 2014). Conflict among people about cats is prevalent in some societies, where human populations have been crudely divided into those who value cats as companions and pest controllers, and those who value wildlife and are concerned about cats as predators and invasive pests (van Heezik 2010, Marra & Santella 2016, Loss et al. 2018). Although vibrantly expressed in contemporary debate, this duality in popular characterisations of cats and their impacts is associated with a more fundamental tension between natural

selection for predatory independence in the wild and artificial selection for affectionate dependence in companion animals (Crowley et al. 2020a).

Cat populations encompass degrees of domestication, varying from one individual to another, as well as with local ecological and cultural conditions (Turner & Bateson 2014). Arguably, complete domestication, consisting of high-level dependence and anthropogenic control of breeding, is apparent only in some pedigree breeds (Bradshaw et al. 1999). Several terminologies are used to describe the degree of domestication of individual cats and, to some extent, their populations, primarily based on their degree of dependence upon humans: Bradshaw et al.

(1999) define pedigree, pet, semi-feral, feral and pseudo-wild cats, while Sparkes et al. (2013) distinguish household, stray or abandoned, street or community, and feral cats. The lack of a uniform definition is clear, for example, in the varying use of the term 'feral', in different countries. In New Zealand and on other islands where cats are perceived as invasive, feral refers to cat populations living and breeding in a wild state (Farnworth et al. 2010). By contrast, in the USA, feral refers to abandoned, stray or unowned cats (Loyd & Hernandez 2012). We follow our earlier classification (Crowley et al. 2020a) of domestic cats, according to the degree of human 'ownership' and the degree of human control over food provisioning, reproduction and movement. By this classification, for example, feral cats are unowned and not subject to control of provisioning, reproduction or movement.

The domestic cat retains a behavioural repertoire that makes some individuals very successful when living independently of people, and all cat populations show a degree of genotypic and phenotypic flexibility that enables them to move between states within a few generations, or even within a lifetime (Bradshaw et al. 1999). Cats' abilities to hunt are among the most important characteristics that have been maintained throughout their evolution, and it underpins their ability to survive in diverse ecosystems. For example, in island ecosystems, feral cats hunt for survival and are major threats to biodiversity (Medina et al. 2011, Palmas et al. 2017). On islands, impacts of cats are amplified, relative to continental areas, due to the evolution of endemic prey species in the absence of terrestrial predators (Bonnaud et al. 2012,

Woinarski et al. 2017). Currently, cats on islands are most often characterised as pests, perhaps ironically, given that most were introduced to such islands to control rodent pests (Driscoll et al. 2009a).

Estimations of the scale of killing by cats suggest that, when abundant, they can be responsible for large numbers of wild animal deaths (Woods et al. 2003, Blancher 2013, Loss et al. 2013, Murphy et al. 2019). Determining the relative importance of compensatory (Møller & Erritzøe 2000, Baker et al. 2005) and additive (van Heezik et al. 2010) effects of predation by cats on prey populations remains a challenge, but Loss and Marra (2017) gathered considerable evidence of indoor–outdoor, free-ranging and feral cats affecting continental vertebrate populations. Beyond their direct effects, cats are implicated in indirect, sub-lethal effects (Beckerman et al. 2007), including reduction of parental care and facilitation of nest predation (Bonnington et al. 2013), competition (Pavey et al. 2008) and disease transmission (Honnold et al. 2005, Eymann et al. 2006).

Numerous caveats notwithstanding, prey animals brought home by owned cats are tangible evidence that some individuals remain proficient hunters. Owned cats no longer need to hunt for survival, though instinct may mean they still feel such a need. The factors affecting variation in hunting are less well understood. Bradshaw et al. (1999) suggested three factors that may have acted to ensure that cats can switch between independence, commensalism and symbiosis with people: "(1) the probability that diets provided by people were [until the 1980s] unlikely to meet their nutritional requirements; (2) the small number of generations that

Table1. Summary of drivers and facilitators of hunting behaviour in cats and their biological implications

Driver/facilitator of hunting	Biological implications	
Evolutionary origins	<i>Felis silvestris lybica</i> : <ul style="list-style-type: none"> • Obligate carnivore • Solitary hunter • Territorial predator catching multiple prey items per day 	<i>Felis catus</i> : <ul style="list-style-type: none"> • Obligate carnivore • Solitary hunter • Surplus killing
Diet	<ul style="list-style-type: none"> • Hypercarnivorous (obligate carnivore) • Able to regulate calorific intake 	<ul style="list-style-type: none"> • Unable to synthesise essential nutrients found in wild prey • High protein requirement • No requirement for carbohydrates in adults • Predation may address deficiencies
Early life history	<ul style="list-style-type: none"> • Kitten introduced to hunting by the mother 	<ul style="list-style-type: none"> • Mother influences kitten prey preferences • Adult prey specialisation
Personality	<ul style="list-style-type: none"> • Individual behavioural variation 	<ul style="list-style-type: none"> • Individual variation in hunting rates and strategies
Environment	<ul style="list-style-type: none"> • Availability and diversity of food sources • Purpose of cat ownership • Cat motivational state for hunting 	<ul style="list-style-type: none"> • Islands: feral cats hunt for survival; endemic species susceptible • Mainland: feral cats exploit anthropogenic food; populations not closely regulated by prey availability • Farms: free-roaming cats as pest controllers • Kept hungry to maximise hunting; subject to prey fluctuations • Urban areas: free-roaming pet cats, independent of prey availability

have elapsed since domestication began, and (3) the historical dual role of cats as pest controllers and companions". Extending from these three factors, we have reviewed a broad literature and identified a range of potential drivers and facilitators of hunting behaviour in cats. We define hunting behaviour as all behaviours forming part of finding and killing live prey, rather than its scale or impact. We organised our review into five factors: evolutionary origins, diet, early life history, personality and environment (Table 1), that either drive or facilitate hunting behaviour. We then reviewed approaches to mitigating any effects of predation by cats of wildlife and indicated their effectiveness, feasibility and welfare implications. We cover cats as owned, companion animals (pets) and as semi-owned and unowned animals. For domesticated species, and for few more so than cats, human–animal relationships are profound. Management can therefore be as much a social as a biological challenge, and the social aspects of cat management merit their own review. We suggest that a better understanding of hunting behaviour in cats could support the development of, and inform debates about, approaches to management. We hope that some of these might open ways for collaboration between advocates both for cats and for wildlife.

METHODS

We searched Web of Science and Google Scholar, using terms including cat, *Felis catus*, domestic, feral, hunting, diet, predation, behaviour, personality, ontogeny, nutrition, evolution, management and invasive species. We assessed books on cats and their biology. We followed articles cited by and citing the located literature.

DRIVERS AND FACILITATORS OF HUNTING BEHAVIOUR

Evolutionary origins

Felis catus is a member of the order Carnivora and family Felidae and descends primarily from Near-Eastern wildcats *Felis silvestris lybica* (Driscoll et al. 2007). The history of domestic associations began ~10000 years ago, when it is thought the species became increasingly commensal and cats' hunting abilities were appreciated by humans as a means of controlling rodent populations in food stores (Driscoll et al. 2009a; Table 1). Both Near-Eastern and Egyptian cat lineages have contributed at different times to the worldwide gene pool of domestic cats (Ottoni et al. 2017). Domestication has been a long-term process, where frequent and long-range translocations by people facilitated mixture between geographically distant

populations (Ottoni et al. 2017). Unlike the domestic dog *Canis familiaris*, which has undergone strong artificial selection, the domestic cat remains largely a product of natural selection (Driscoll et al. 2009b). It remains morphologically (Yamaguchi et al. 2004), physiologically and behaviourally similar in most respects to its progenitor: a solitary, territorial and obligate carnivore that kills several small animals per day (Bradshaw 2006, 2016). The very recent history of 'true' domestication, beginning perhaps as little as ~200 years ago, means that domestic cats effectively remain genetically 'wild' (Tamazian et al. 2014). Few genomic alterations in domestic cats are attributable to domestication, excepting genes affecting memory, fear-conditioning and reward learning (Montague et al. 2014). Domestic cats have retained the genetic basis for effective hunting (Bradshaw 2006), including sensory traits such as a broad hearing frequency range, high visual acuity and accentuated vomeronasal capacity (Montague et al. 2014). Critically, in relation to augmented impacts upon prey, cats maintain separation between hunting motivation and prey consumption (Leyhausen et al. 1956) and do not necessarily eat what they kill. Adamec (1976) observed that hungry cats would leave palatable food in order to kill live prey, but would then return to provisioned food. This is likely to increase food input by providing for multiple kills when opportunities arise (Adamec 1976, Macdonald et al. 1984), and surplus killing has been documented in feral (McGregor et al. 2015) and owned cats (Lloyd et al. 2013).

Diet

Domestic cats are obligate carnivores in terms of nutrient requirements, ingestion, digestion and metabolism (Bradshaw et al. 1996; Table 1). The narrow carnivory expressed by all Felidae, and their nutritional peculiarities (Macdonald et al. 1984), relate to ancestral loss of metabolic enzymes, including those involved in synthesis of vitamin A, prostaglandin, taurine and arginine. In the feline genome, genes implicated in lipid metabolism are enriched (over-represented among differentially expressed genes), further indicating adaptation to obligate carnivory (Cho et al. 2013). Cats' requirement for high-protein diets derives from lack of regulation of aminotransferases in dispensable nitrogen metabolism and urea cycle enzymes (Rogers et al. 1977, Rogers & Morris 1980, Morris 2001). Similarly, the requirement for dietary niacin is related to picolinic carboxylase activity (Suhadolnik et al. 1957), while requirements for vitamin D relate to 7-dehydrocholesterol- Δ^7 -reductase activity (Morris 2001). Unlike in kittens, there is no dietary requirement for carbohydrates in adult cats (Macdonald et al. 1984).

The nutrients cats require are all found in wild prey. Dietary analyses of feral cats show that among wild foods,

they mainly eat small mammals, with smaller contributions from birds, herpetofauna and insects, and take multiple small meals of high protein content per day (Bonnaud et al. 2007, Medina & Nogales 2008, Faulquier et al. 2009, Ozella et al. 2016). While some owned cats fed from birth on nutritionally complete food are characterised as ‘fussy’, in exhibiting neophobia towards novel foods (Bradshaw et al. 2000), others exhibit catholic diets. Cats modify their prey preferences to support a balanced diet (Bradshaw 2006), and dietary diversity in feral and free-ranging cats is maintained by (anti-apostatic) selection of rarer food items (Church et al. 1994, Bradshaw et al. 2000). Maintaining dietary diversity appears to be an adaptive means of addressing specific nutritional demands. Many owners feed their cats once or twice a day, sometimes giving more than their cats can eat in a single meal (Kaufman et al. 1980). When owned cats have ad libitum access to food, they eat 7–20 small meals daily (Mugford 1977), more closely resembling wild-type feeding patterns, hence feeding other than ad libitum might prompt more frequent hunting.

Over the last half-century, cats’ requirements for specific nutrients have been increasingly well understood, and, since the 1980s, improvements have been implemented by pet food manufacturers. Owned cats can, in principle, now rely on human provisioning to obtain a ‘balanced’, ‘complete’ diet. Nevertheless, commercial pet food bears little resemblance to natural prey, having lower energy density and different sensory properties (Bradshaw 2006). Moreover, because natural prey is high in protein and scarce in carbohydrates, and most cat foods are rich in starches, it has been speculated that high-carbohydrate pet foods could be detrimental for cat health (Verbrugghe & Hesta 2017). Outdoor access (Defauw et al. 2011) and taking wild prey are protective of urinary tract disease, and this effect interacts with dry food provision, leading to hypotheses that cats fed a high proportion of dry food might seek alternative, wild prey (Jones et al. 1997). Direct provision by people of any food to cats is a very recent attribute of domestication and, with only the very recent advent of complete diets, selection is likely to have favoured maintaining hunting ability to obtain essential, but otherwise scarce, nutrients. The specific dietary requirements of cats, together with variation in the quality, quantity and availability of wild and provisioned foods, are therefore likely to be significant drivers of variation in hunting behaviour and predation rates.

Early life history

The early development of kitten behaviour plays an important role in forming adult behaviour, individuality and sociability towards humans (‘friendliness’; McCune

et al. 1995, Ahola et al. 2017, Table 1). In the wild, kittens are introduced to hunting by their mother creating situations in which they hone hunting skills (Bateson 2000). Kittens tend to follow maternal prey choices, and young cats acquire skills through social learning (Kuo 1930). Adult cats are better able to catch particular prey if they had experience of that prey as kittens, but being more skilful in catching one prey does not engender a general improvement in hunting skills (Caro 1980a). Life history shapes individuality in hunting technique and prey specialisation, and this has gained attention as a means of focusing management upon ‘problem individuals’ (Dickman & Newsome 2015, Moseby et al. 2015, Swan et al. 2017).

Similarities between hunting and playing behavioural sequences suggest that play behaviours are linked to hunting skill. Play is not, however, required for developing basic elements of hunting behaviour. At 11 weeks, cats reared in social isolation showed normal predatory responses when presented with prey-like stimuli (Thomas & Schaller 1954) and early-life object play does not affect adult predatory skills (Caro 1980b). However, play and hunting behaviour both increase towards the end of weaning, alongside declining social play, suggesting that this change characterises impending independence from the natal environment (Bateson & Barrett 1978). Owners can engage their cats in various forms of interactive object play, with wands, fishing toys, laser pointers, balls, etc. Such play involves the reproduction of elements of the predatory sequence, and different types of play might conceivably be associated with development of prey preference or specialisation, which can impose a pressure on small populations of prey species (Scrimgeour et al. 2012). Contact in early life influences cats’ tolerance of people; ‘friendliness’ towards humans is genetically influenced, but experientially determined during socialisation at 2–12 weeks (Turner et al. 1986, McCune 1995). Lack of association with humans would produce cats that are less suited to being pets and more likely to be self-reliant foragers, whether by hunting or by exploiting foods accidentally or deliberately provided by humans.

Personality

Individual cats exhibit remarkable variation in hunting rates and strategies (Kays & DeWan 2004, Tschanz et al. 2011, Thomas et al. 2012, Loyd et al. 2013, Table 1). Such marked individual variation is a key element of cat personality, where personality refers to differences in behavioural patterns, consistently expressed across multiple contexts, that distinguish one animal from others of similar sex, age or class (Lowe & Bradshaw 2001). Individual behavioural differences are well described in cats (McCune

1995) and a personality structure has been developed for captive Scottish wildcats *Felis silvestris grampia* (Gartner & Weiss 2013). Building on the wildcat study, Litchfield et al. (2017), in a study involving almost 3000 owned cats, determined that personality profiles map across 'the feline five' (comparable with the 'Big Five' human personality traits; Digman 1990): neuroticism, extraversion, dominance, impulsiveness and agreeableness. Cats exhibiting certain of these personality types, perhaps most likely low neuroticism (boldness, leading to travelling, exploring) or high extraversion (curiosity, leading to boredom; Litchfield et al. 2017), would potentially be more interested in hunting wild prey, but there has not yet been any investigation of personality and hunting.

Links between personality and coat colour and pattern have been proposed. Tricoloured cats (calicos, tortoiseshells) are perceived to be more intolerant and aloof, while ginger and bicoloured cats are considered to be particularly friendly (Delgado et al. 2012, Stelow et al. 2016). Associations between coat pattern and personality are weak, however, suggesting little association between genes influencing coat and behavioural phenotypes. An exception is apparent for ginger cats, which exhibit greater interest in prey (Wilhelmy et al. 2016). This might also align with their relative abundance in rural areas and suggests links between the genetic underpinnings of behavioural variation among coat polymorphisms (Garcia 1990, Pontier et al. 1995).

Environment

Different environments provide varying availabilities and diversities of food, in terms of species, abundance, accessibility and prey animals' avoidance of predation (Table 1). Cats are generally considered to be opportunistic hunters that are adaptable to seasonal fluctuations in prey abundance (Krauze-Gryz et al. 2017), and this is particularly evident on islands populated by feral cats that tolerate variation in the availability of non-native and native prey (Genovesi et al. 1995, Nogales & Medina 2009, Bonnaud et al. 2011a, Ozella et al. 2016). Island endemic species are especially vulnerable to predation by cats (Fitzgerald 1988), and when breeding seabirds are present, they become important secondary prey (after introduced mammals; Keitt et al. 2002, Bonnaud et al. 2011b).

Feral cats are widely established in continental areas characterised by high diversity of wild prey species. In addition to wild prey, feral cats take food accidentally or deliberately provided by humans (Bradshaw et al. 1999). Provisioned populations are less regulated by fluctuations in wild prey, leading to hyperpredation, as their densities may exceed local, 'natural' carrying capacity (Courchamp et al. 2000).

For owned, free-ranging cats, their lifestyles, hunting motivations and opportunities are affected by their husbandry and location in urban or rural ecosystems. Cats living on farms, and many of those in rural environments, are kept for their ancestral role as rodent controllers, and their survival relies on prey availability. Indeed, some farmers have believed that keeping cats undernourished makes them better hunters (Tabor 1983). Hungry cats do hunt more (Kays & DeWan 2004, Silva-Rodriguez & Sieving 2011), and hunger can reduce attachment to their residence (Fitzgerald & Turner 2000). In contrast, owned urban cats are generally well-fed, and survival and density vary independently of wild prey availability (Thomas et al. 2014). Differences in the composition of prey brought home in rural and urban areas probably reflect local prey availability, driven by differences in land use. The diets of cats on farms exhibit temporal variation according to seasonal variability in small mammal populations, while bird captures are more frequent among urban cats, reflecting the relative abundance of resident garden birds (Kauhala et al. 2015, Krauze-Gryz et al. 2017). This might alternatively reflect variation in the tendency to keep owned cats in urban areas inside at night, when small mammals are more active (Woods et al. 2003) and wider ranging by rural cats (Hanmer et al. 2017). Densities of cats in urban areas are high and increase with housing density, imposing local pressure on prey populations (Baker et al. 2005, Sims et al. 2008, Thomas et al. 2012). Social factors and environmental characteristics influence densities of urban cats, particularly unowned cats. In New Zealand, residential areas with higher human density and a high deprivation index host greater numbers of aggregations of unowned cats (Aguilar & Farnworth 2012, 2013).

MANAGEMENT APPROACHES

Numerous approaches to management have been advocated and adopted for reducing the direct and indirect effects of cats upon wildlife. This is an extensive topic, with particularly detailed and valuable accounts for Australia (Doherty et al. 2017, Woinarski et al. 2019) and the USA (Marra & Santella 2016, Loss et al. 2018). We outline what each management approach involves, its effectiveness, feasibility in different environments and implications for cat welfare. We have identified five categories of approach (Fig. 1; Table 2): lethal control, non-lethal control (largely involving control of reproduction), inhibition (involving various devices and deterrents), access management and enrichment (involving improvements to welfare, health and nutrition).

Lethal control

Lethal control is considered to be indispensable for predator eradication on islands (Russell et al. 2016). For cats, lethal

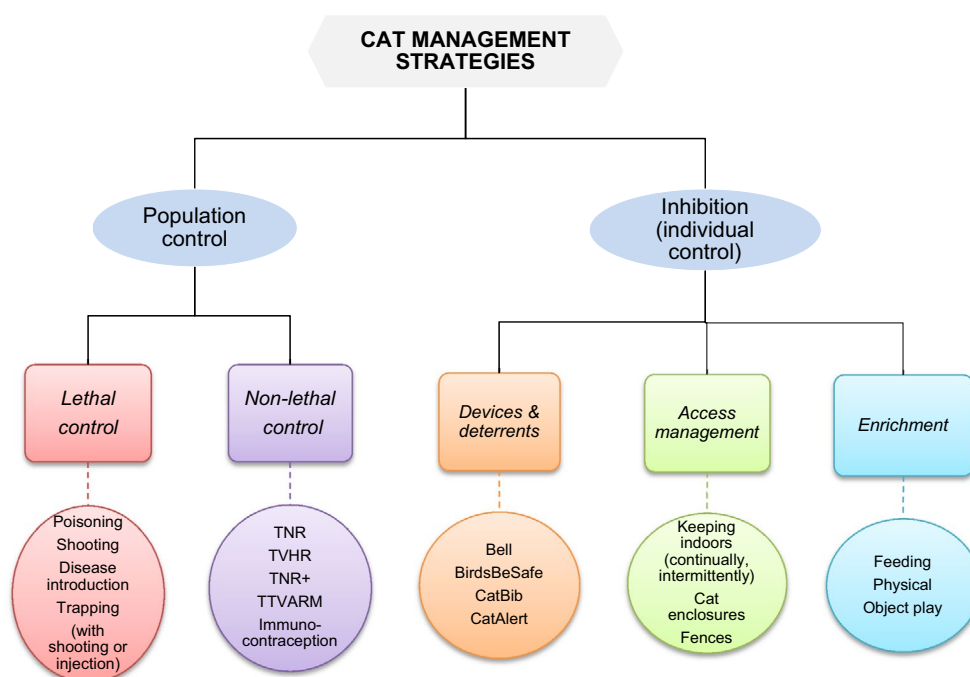


Fig. 1. Schematic showing management approaches for cat populations and individuals. Non-lethal approaches to population control are largely based on trap–neuter–return (TNR) and variants thereof, including trap–vasectomy–hysterectomy–return (TVHR), TNR with removal of kittens for adoption (TNR+) and trap–test–vaccinate–alter–return–monitor (TTVARM). [Colour figure can be viewed at wileyonlinelibrary.com]

Table 2. Summary of management approaches for reducing predation of wildlife by cats, through cat population control and individual interventions (tick = applied, cross = not generally applied)

Management approaches	Feral cats		Free-ranging owned cats		
	Islands	Mainland	Islands	Farms	Urban areas
Lethal control					
Poisoning	✓	✗	✗	✗	✗
Shooting	✓	✓	✗	✗	✗
Disease introduction	✓	✗	✗	✗	✗
Trapping then shooting	✓	✗	✗	✗	✗
Trapping then injection	✓	✓	✓	✓	✓
Non-lethal control					
Trap–neuter–return and variants	✗	✓	✓	✓	✓
Immunocontraception	✗	✗	✓	✓	✓
Devices and deterrents					
Bell	✗	✗	✗	✗	✓
BirdsBeSafe (brightly coloured collar cover)	✗	✗	✗	✗	✓
CatBib	✗	✗	✗	✗	✓
CatAlert (sonic warning device)	✗	✗	✗	✗	✓
Access management					
Indoors at sunrise and dusk	✗	✗	✓	✗	✓
Indoors	✗	✗	✓	✗	✓
Fence	✓	✓	✗	✗	✗
Cat enclosures (cat patio, catio)	✗	✗	✗	✗	✓
Enrichment					
Feeding	✗	✗	✗	✗	✓
Physical	✗	✗	✗	✗	✓
Object play (playtime)	✗	✗	✗	✗	✓

Table 3. Summary of methods used in lethal population control of cats

Lethal method	Time to death	Modes of action	Welfare implications
Toxin: Sodium fluoroacetate (1080)	24 h	Interferes with cellular energy production and inhibition of tricarboxylic acid cycle	Disorientation, vocalisations and vomiting, immobile for several hours before death
Toxin: Para-aminopropiophenone (PAPP)	37–246 min	Causes methaemoglobinaemia (elevated blood methaemoglobin)	Central nervous system anoxia and lethargy, rapid loss of consciousness and rapid death
Biocontrol: Feline panleukopaemia virus	2–10 days	Infects and kills growing and dividing cells (bone marrow, intestines and foetus). Fall in white blood cells.	Loss of appetite, avoidance and inactivity, pain, fever, lethargy, vomiting, diarrhoea, discharge and dehydration
Direct killing: trapping, hunting and shooting/ euthanasia	Related to time elapsed before euthanasia; death occurs within seconds/minutes	Euthanasia (central nervous system)	Stress during time of latency in trap

control methods include trapping (cage traps, paw traps, leg-hold traps), hunting with dogs, shooting, poisoning and introducing diseases (Nogales et al. 2004; Tables 2 and 3). Up to October 2020, feral cats have been eradicated from 107 islands, while 19 attempts have failed (DIISE 2020), reportedly due to lack of planning, inappropriate methods and failure of local support (Campbell et al. 2011). Each eradication employed combined methods, but all successful programmes relied upon poisoning. The most widely used toxicant for cats is sodium fluoroacetate (1080), though its extreme toxicity and risks of non-target and secondary exposure (Eisler 1995) have led to restrictions on use. Para-aminopropiophenone (PAPP) has been developed and successfully tested in New Zealand as a more humane toxin that targets carnivores, including cats (Murphy et al. 2007).

Trapping and shooting can complement chemical controls, and applying multiple, independent methods appears to be essential for the control of residual individuals (Nogales et al. 2004). With intense effort and favourable terrain, trapping may facilitate eradication from small islands. Otherwise, cage traps are used in capture for euthanasia, sterilisation or live removal (Hanson et al. 2010), or when non-target casualties, including of owned cats, are unacceptable. Captured feral cats may be killed by shooting, lethal injection or carbon dioxide gas (Rocamora & Henriette 2015), though the latter is associated with welfare concerns (Simonsen et al. 1981). Trapping (particularly leg-hold trapping) causes injuries to non-target animals, posing ethical concerns, especially for threatened species (Surtees et al. 2019). Shooting is a labour-intensive method, preferentially applied in small areas or in targeting problematic, or residual, individuals (Moseby et al. 2015).

The biological control of cats has primarily been through introductions of feline viruses. Feline panleukopenia virus was successfully applied in eradication campaigns on Marion Island, Indian Ocean, and Jarvis Island, South Pacific Ocean (Nogales et al. 2004).

Some highly effective lethal methods, including biological control and some toxicants, are markedly inhumane, due to the severity of distress or pain experienced before death (Table 3). Symptoms of 1080 include disorientation, uncoordinated movements, vocalisations and vomiting. Cats become lethargic and immobile for several hours before death, which occurs up to 24 hours after exposure (Eason & Frampton 1991). By comparison, PAPP is considered relatively humane; it causes death by methaemoglobinaemia, resulting in central nervous system anoxia, rapid loss of consciousness and rapid death (Eason et al. 2010). Viral infections compromise welfare over extended periods. Sickness due to feline parvovirus is associated with pain, high fever, lethargy, vomiting, severe bloody diarrhoea, discharge and dehydration. More humane methods in lethal control are shooting and euthanasia, which provide more rapid, less painful deaths, though prolonged containment in traps compromises welfare.

Cat eradications generally bring major direct benefits to island faunas (Jones et al. 2016) and further permit the restoration of native taxa locally extirpated by cats (Algar et al. 2020). However, unexpected trophic cascades arising from cat removal can be environmentally and economically costly. On Little Barrier Island, New Zealand, cat removal resulted in reduced breeding success of Cook's petrel *Pterodroma cookii* due to increased predation by rats *Rattus* spp. (Rayner et al. 2007). On Macquarie Island, Pacific Ocean, cat eradication precipitated a trophic cascade leading to rapid landscape and ecosystem changes, due to increased rabbit *Oryctolagus cuniculus* populations (Bergstrom et al. 2009).

On inhabited islands, human residents often contribute directly to unowned cat populations by not sterilising their cats and by abandoning unwanted kittens and adults (Medina et al. 2016), so regulation of owned animals is required to eradicate unowned cats. Regulatory measures include sterilisation, identification, registration and control of importation

(Nogales et al. 2013). Such measures are being implemented on Ascension Island, South Atlantic Ocean, under a 'Dogs and Cats Ordinance', with fines for non-compliance. In strict campaigns, such as on Baltra Island, Galápagos Islands, owning cats as companion animals is prohibited, and existing pets were translocated or euthanised (Campbell et al. 2011). In continental areas, eradication of feral cats is difficult because of the challenges of using toxins in human settlements. Consequently, the most common lethal method used for reducing populations in settled areas is trapping and euthanasia (Tan et al. 2017).

Non-lethal control

Non-lethal control approaches aim for reduction in cat numbers over several years (Levy et al. 2003). Control of reproduction can be achieved through surgical methods (neutering of males and females; spaying of females) or non-surgical methods (contraceptives; Table 2). Surgical procedures are carried out via trap–neuter–return (TNR), trap–neuter–relocate (to farms, sanctuaries or the mainland in the case of islands) and variants. Controlling cat populations via TNR is possible, but requires sterilisation rates of 51–94% (Andersen et al. 2004, Schmidt et al. 2009, McCarthy et al. 2013). Intensive TNR and adoption of socialised cats and kittens can reduce colony size (by around 31%), improve welfare and reduce cat intake to shelters (Levy et al. 2014, Tan et al. 2017, Spehar & Wolf 2018) and can markedly reduce 'preventable' cat deaths (Boone et al. 2019). TNR has also proven comparable, in cost terms, to lethal control by trapping, but with benefits in terms of reduced complaints about cats and impoundments of cats (Hughes et al. 2002). The inefficiency of TNR for managing large populations has generated disapproval among conservation organisations (Longcore et al. 2009, Loss & Marra 2017). The approach requires intense effort and often relies on volunteers, so sustaining control and assessing outcomes are problematic (Robertson 2008) over anything more than small geographic areas (Crawford et al. 2019), e.g. a university campus of 5.7 km² (Levy et al. 2014) and a docklands area of 0.8 km² (Spehar & Wolf 2017). Moreover, the ecological benefits derived from neutering campaigns are uncertain (Guttilla & Stapp 2010) and there are no scientific studies of the effect of sterilisation on predation.

Of non-surgical methods, a promising avenue is immunocontraception, which, in principle, induces long-term or permanent sterility after a single treatment. In principle, it is less costly, less technically demanding and less invasive than surgery (Levy et al. 2011). GonaCon is a gonadotropin-releasing hormone vaccine that was tested on laboratory cats and provides effective fertility control over multiple years with a single dose. However, granulomatous masses at the injection site were observed in 33% of treated cats

two years after injection (Levy et al. 2011). Unfortunately, tests of a safer, modified vaccine, showed that a single dose of GonaCon did not provide contraception for a sufficient proportion of female cats living under colony conditions (Fischer et al. 2018). Thus, although the approach is promising, no immunocontraceptives for cats are yet available.

Inhibition

Various devices and deterrents have been developed and commercialised to reduce predation (Table 2). Fitting owned cats with a collar with a bell has diverse outcomes, with no effects on predation rates in Australia (Barratt 1997), but significant reduction in prey returns by 50%, at least in the short term, in the UK (Ruxton et al. 2002, Nelson et al. 2005) and New Zealand (Gordon et al. 2010). Woods et al. (2003) found that bells were associated with lower reported rates of predation on mammals, but not birds, speculating that birds relied on visual cues to avoid predators. Over the long term, cats may compensate for any hunting handicap arising from wearing a bell by modifying hunting strategies (Nelson et al. 2005). CatAlert (Willana Life Sciences), a collar-mounted sonic warning device, reduces prey rates by 38% for mammals and by 51% for birds (Nelson et al. 2005). CatBib (www.catgo.ods.com) is a 'pounce protector' bib attached to a collar, which, in a single trial, stopped 81% of cats catching birds, 33% catching herpetofauna and 45% catching mammals (Calver et al. 2007). BirdsBeSafe (www.birdsbesafe.com) is a brightly coloured collar cover that reduces bird-killing [0.72 birds per year with BirdsBeSafe and 5.56 without (Willson et al. 2015); 0.44 birds per month with BirdsBeSafe and 1.89 without (Pemberton & Ruxton 2019)]. Cats wearing rainbow-patterned BirdsBeSafe showed a greater reduction than those wearing the collar covers with other patterns in the number of prey with colour vision (birds and herpetofauna) brought home (Hall et al. 2015). All such device trials acknowledge a reliance on numbers of animals brought home by cats as a proxy for the frequency of killing, which camera studies suggest is likely to be an underestimate (Lloyd et al. 2013).

Irrespective of their successes in reducing killing, inhibitory devices may not prevent indirect effects on prey populations. Moreover, cat owners seem reluctant to use inhibitory measures to reduce hunting, especially when conservation benefits do not accord with their priorities for cat welfare (Hall et al. 2016, Harrod et al. 2016, Crowley et al. 2019, 2020b).

Access management

Owners can eliminate or reduce hunting opportunity by restricting cats' access to the outdoors, by keeping them

indoors at night or at dawn and dusk when birds are most active (Table 2). Owners variously see confinement as beneficial in reducing the risk of fighting, theft and road accidents or as detrimental to cat welfare or to pest control functions, if nocturnal confinement reduces capture of target rodents or non-native species (Crowley et al. 2019, 2020b, Linklater et al. 2019). Other available options for controlling cat outdoor access are exclusion fencing, cat patios ('catios', e.g. ProtectaPet), leash or harness walks and tie-outs (Tan et al. 2020). Fencing is, however, primarily used to prevent incursions by feral cats to protected areas, and use in Australia and New Zealand is widespread and effective (Moseby & Read 2006). Fenced exclusion zones have been also established in urban habitats (e.g. Zealandia in Wellington and Mulligans Flat in Canberra). Cat exclusion zones have also been proposed in rural areas and in protected areas close to human settlements (Metsers et al. 2010).

Enrichment

Enrichment implies an improvement in animal welfare, measurable in terms of increased lifetime, reproductive success or health, through modifications of environment or husbandry (Newberry 1995, Ellis 2009). Enrichment approaches for owned and semi-owned cats that might affect hunting of wildlife, by affecting stimuli relating to nutrition, foraging and hunting, include: reproducing natural foraging behaviours, hiding food, using 'puzzle' feeders and engaging cats in play simulations of hunting sequences (Ellis 2009; Table 2). Direct nutritional enrichment might also involve manipulations of the frequency of feeding, food quantity, quality and content, to ensure provision of essential nutrients (Bloomsmith et al. 1991). Given the specificities of cat nutritional requirements outlined above, this avenue holds particular research potential for reducing any motivations for hunting deriving from nutritional deficiency, not least because of the apparent disconnect between motivation and prey consumption (Leyhausen et al. 1956). Indoor environments can be enriched by physical modifications (cat trees, scratching posts, hiding places) and provision of appropriate feeding, drinking, toileting and rest areas (Ellis et al. 2013). Dedicated playtime keeps cats active, resulting in a reduction of common behavioural problems (Strickler & Shull 2014). Little research has been undertaken to investigate the link between environmental or nutritional enrichment and hunting rates. Providing litter boxes and hiding places was significantly associated with reduced numbers of prey brought home by indoor-outdoor cats (Escobar-Aguirre et al. 2019), thus it may be the case that enhancing the cat's environment and overall well-being leads to variation in hunting activities, opening

the possibility to adopt beneficial interventions as novel management approaches.

CONCLUSIONS

Domestic cats are abundant and near-ubiquitous predators. Whether they are feral or are indoor companions, modern cats display the inherited influence of their wild ancestors on morphology, physiology and behaviour. The most apparent elements of this evolutionary legacy relate to feeding, comprising their obligate hypercarnivorous diet, solitary hunting activity and feeding patterns. Marked between-individual variation in hunting behaviour is likely to be part of cat personality, though it seems difficult to link it to other phenotypic traits. Environment and opportunity have powerful impacts on both frequency and effectiveness of hunting behaviour by cats.

In response to the actual and perceived impacts of cats upon wild prey populations, various management approaches have been adopted to control cat populations and hunting behaviour: lethal control methods, non-lethal control methods that tend to stabilise densities but rarely reduce them, and devices, deterrents and restrictions that use inhibition and access restrictions with the aim of reducing the success of hunting by cats. Enrichment remains largely untested as a means of reducing hunting, but indications of association between environment and hunting behaviour suggest the potential of this approach.

Few researchers have highlighted the drivers of the retention of hunting behaviour or have attempted to reduce predation rates by working with strategies that relate to or build on their evolutionary origins. Hunger increases cats' motivation for both play (Hall & Bradshaw 1998) and predatory behaviour, suggesting that play and predation share common elements (Biben 1979, Hall & Bradshaw 1998). Being an obligate carnivore implies requirements for high protein, associated with high activity of nitrogen catabolic enzymes and loss of metabolic enzymes or pathways involved in the synthesis of essential nutrients. In nature, strict nutritional requirements are addressed by a diet consisting of animal prey (Bradshaw 2006). With the advent of commercial pet food manufacture, owners can, in principle, provide a complete diet to their cats, which fulfils their macronutrient, micronutrient and amino acid requirements. Nevertheless, some nutrients may be diminished or lost during manufacturing, some foods rely on plant protein sources, potentially compromising bioavailability of amino acids (Kanakubo et al. 2015), and some brands do not meet all micronutrient recommendations (Davies et al. 2017, Brunetto et al. 2019). Thus, we accord with Bradshaw et al. (1999) that a selective advantage of retaining wild behaviours arose from "the probability that diets provided by people were unlikely to meet their

nutritional requirements". We hypothesise that variation in diet quality, as well as quantity (Silva-Rodriguez & Sieving 2011), has the potential to drive between-individual variation in hunting by provisioned cats. Enhancing the quality of nutrition of the world's owned cats therefore merits further investigation as a means of addressing predation of wildlife by domestic cats, while also improving cat health and welfare.

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